

Seasonal variation and partitioning of ecosystem respiration in a southern boreal aspen forest

T.J. Griffis^{a,*}, T.A. Black^a, D. Gaumont-Guay^a, G.B. Drewitt^a,
Z. Nescic^a, A.G. Barr^b, K. Morgenstern^a, N. Kljun^a

^a Faculty of Agricultural Sciences, Biometeorology and Soil Physics Group, University of British Columbia, Vancouver, BC, Canada V6T 1Z4

^b Climate Research Branch, Meteorological Service of Canada, 11 Innovation Blvd, Saskatoon, Sask., Canada S7N 3H5

Received 3 November 2003; received in revised form 14 April 2004; accepted 27 April 2004

Abstract

Continuous automatic chamber and eddy covariance (EC) measurements were made at an old aspen forest (SOA) located at southern boreal treeline in Saskatchewan, Canada to examine the temporal variability in soil (R_s), tree bole (R_b), and ecosystem respiration (R_E) during 2001. Climatic conditions were significantly warmer and drier than the 30-year climate normal, resulting in lower R_E and an unprecedented increase in net ecosystem productivity (NEP). In the 7-year record (1994, and 1996–2001) of CO_2 exchange at SOA, the year 2001 showed the greatest carbon gain ($300 \text{ g C m}^{-2} \text{ year}$). Scaled chamber measurements ($1315 \text{ g C m}^{-2} \text{ per year}$) were 37% larger than the EC estimate of R_E ($961 \text{ g C m}^{-2} \text{ per year}$). The difference between the scaled chambers and the EC estimate was reduced to 20% after correcting for lack of energy balance closure. Annual R_E was approximately $170 \text{ g C m}^{-2} \text{ per year}$ lower than the average of the previous 6 years. Annual estimates of microbial-heterotrophic (R_h) ($510 \text{ g C m}^{-2} \text{ per year}$) and autotrophic respiration (R_a) ($805 \text{ g C m}^{-2} \text{ per year}$), based on chamber measurements, were used to help validate the EC estimate of R_E . R_a represented 61% of the total chamber respiration. This fraction was used to partition R_E into R_a and R_h to calculate net primary production (NPP). The values of NEP ($300 \text{ g C m}^{-2} \text{ per year}$) and NPP ($675 \text{ g C m}^{-2} \text{ per year}$) were more characteristic of temperate forests. The NPP/ P_g ratio of 0.54 was within the range of recently published values using biometric techniques and supports that the annual ecosystem respiration budget and its partitioning was well constrained. We recognize, however, that this ratio will vary interannually depending on climatic conditions. In 7 years of annual EC CO_2 flux measurements at SOA, this study provides the first evidence that drought can lead to a transient increase in CO_2 sequestration resulting from a reduction of R_E .

© 2004 Elsevier B.V. All rights reserved.

Keywords: Boreal forest; Ecosystem respiration; Automatic chambers; Eddy covariance; Net ecosystem CO_2 exchange; Phenology; Flux partitioning; Net primary production

1. Introduction

Recent developments in measurement techniques have provided the opportunity for long-term monitoring of net ecosystem CO_2 exchange (NEE) at remote field sites using both automatic chambers (Drewitt et al., 2002) and the eddy covariance technique (Black

* Corresponding author. Present address: Department of Soil, Water, and Climate, University of Minnesota, Borlaug Hall, 1991 Upper Buford Circle, St. Paul, MN 55108, USA.
Tel.: +1-612-625-3117; fax: +1-612-625-2208.
E-mail address: tgriffis@umn.edu (T.J. Griffis).

et al., 1996; Baldocchi et al., 2001). The simultaneous deployment of each of these methods on an annual basis is providing unique datasets that offer significant insight into the controls on ecosystem respiration (R_E) and gross ecosystem photosynthesis (P_g). Such developments are important because they offer independent means to constrain annual carbon budgets. Given the recent debate concerning the importance of respiration in determining the sink/source strength of ecosystems (Valentini et al., 2000; Giardina and Ryan, 2000; Grace and Rayment, 2000; Piovesan and Adams, 2001; Jarvis et al., 2001; Janssens et al., 2001), and the potential difficulties of estimating R_E from nighttime micrometeorological measurements (Lee, 1998; Mahrt, 1998), the Boreal Ecosystem Research and Monitoring Sites (BERMS) team (Barr et al., 2002; Griffis et al., 2003) embarked on making continuous multi-year measurements of CO_2 exchange using an automated chamber network to support their long-term eddy covariance program.

This paper examines the effects of climate, phenology and photosynthesis on R_E from a deciduous aspen forest during 2001, a warmer and drier than normal summer. These climatic conditions caused an unexpected and unprecedented increase in the net CO_2 sink strength of this forest (Barr et al., 2004a). The objectives of this paper are to: (1) examine the seasonal variability in respiration measured with both automatic biotic chambers and eddy covariance techniques; (2) assess the influence of weather and climate on soil respiration (R_s), tree bole respiration (R_b) and ecosystem respiration (R_E); (3) study the influence of phenology and photosynthesis on respiration; (4) partition R_E into its heterotrophic and autotrophic components.

2. Methods

2.1. Study site

The forest type chosen for this investigation is aspen (*Populus tremuloides* Michx. and *Populus balsamifera* L.) consisting of a dense hazelnut (*Corylus cornuta* Marsh.) understory. The experimental site was established in 1993 as part of the Boreal Ecosystem-Atmosphere Study (BOREAS) (Sellers et al., 1997). The site is referred to as southern old aspen (SOA) and is located near southern boreal

treeline in Prince Albert National Park (53.629°N, 106.200°W), Saskatchewan, Canada. The surrounding terrain is flat with a slope less than 1% and is relatively homogeneous. The stand age, as of the year 2001, is ~74 years. Stand density is 980 stems ha^{-1} and soil carbon content is approximately 6.7 kg m^{-2} (Gower et al., 1997). The soil texture ranges from loam to clay loam with a 2–10 cm organic layer. The mean annual temperature and precipitation for the site, based on the 30-year climate record 1971–2000 at Waskesiu Lake (53.917°N, 106.083°W), is 0.4 °C and 467 mm, respectively (http://climate.weatheroffice.ec.gc.ca/climate_normals/). Flux measurements have been continuous since 1996 under the Boreal Ecosystem Research and Monitoring Sites Program. Here, we report on measurements made during 2001 and present the first annual comparison of CO_2 fluxes measured simultaneously with automatic chambers and eddy covariance techniques at SOA.

2.2. Automatic chamber measurements

An automatic non-steady-state chamber system (Drewitt et al., 2002) was installed at SOA in July 2000. The system consists of one control box outfitted with two data loggers (Models CR10, 21X Campbell Scientific Inc., Logan, UT, USA), a pump box, five 65-L soil chambers and one 95-L tree bole chamber. The soil chambers are transparent, constructed from acrylic, and were inserted approximately 3–4 cm into the soil. Signal monitoring, timing of measurement events, and data acquisition was performed by the 21X data logger. Communication between the 21X and custom designed relay boards were used to control six chambers. The 21X controlled the timing (opening/closing of each chamber), while the specific control tasks (time to open, lid open/closed logic status and fault status) were carried out by a slave microprocessor (Model Picstic 3, Micromint Corporation, Longwood, FL, USA). After the chamber lid was closed, the chamber air was sampled at 5 Hz and averaged every 5 s over a 5 min interval allowing one complete cycle of chamber measurements to be made every 30 min. The change in CO_2 mixing ratio in each chamber was measured using an infrared gas analyzer (IRGA, Model LI-6262, LI-COR Inc., Lincoln, NE, USA). Sample tubes, 15 m long and 4 mm ID (Dekabon Type 1300, Dekoron, Furon Brands,

Aurora, OH, USA) linked each chamber to a manifold controlled by AC solenoid valves. Chamber air was pulled through the IRGA with an AC linear pump (model SPP-15EBS-101, Gast Manufacturing, Benton Harbor, MI, USA) and cycled back to the chamber through a second solenoid valve manifold and return line. Flow rate through the sample tubes was 8 L min^{-1} giving a relatively short residence time of approximately 4 s. Two small fans inside each chamber ensured that chamber air was well mixed and a 30 cm long 4 mm ID open ended tube allowed pressure equilibration with the atmosphere. The gas analyzer was housed in a thermostatically controlled box and calibrated daily by flowing a known concentration of CO_2 (gain correction) and nitrogen CO_2 free-air (offset correction) through the sample cell of the analyzer. The gain and zero offsets were used to correct the gas analyzer CO_2 mixing ratio offline in flux calculations. The change in CO_2 mixing ratio is dependent on the mass of gas contained in each chamber, which varies with head space, temperature, pressure, small leaks, and as well, adsorption of CO_2 to chamber walls, tubing, vegetation and litter (Drewitt et al., 2002). These volume differences can lead to underestimates in the CO_2 flux. Geometric chamber volumes (V_g) were corrected by measuring temperature and pressure changes, and by observing the departure between a known flux injected into the chamber using a mass flow controller (Model 1179, MKS Instruments, Andover, MA, USA) and the measured flux calculated for the same period. The observed difference was used to compute an effective volume of each chamber two times per day. The effective volume calibration was obtained for three periods (DOY 90–DOY 120, 31 March–30 April; DOY 190–DOY 220, 9 July–8 August; DOY 335–DOY 365, 1–31 December) during the course of the measurement campaign and was on average 16% larger than the geometric volume. Custom software was developed to ensure that signals with high noise were rejected from the flux calculations by testing the statistical significance of changes in CO_2 mixing ratio with time. The soil surface CO_2 efflux (F_{cs}) was calculated from

$$F_{cs} = \frac{\rho_a V_E S_m}{A} \quad (1)$$

where ρ_a is the density of dry air (mol m^{-3}), V_E the effective volume (m^3), A the soil surface area (0.20 m^2)

enclosed by the chamber collar and S_m the rate of change in CO_2 mixing ratio ($\mu\text{mol mol}^{-1} \text{ s}^{-1}$) during the measurement interval. S_m was obtained from the linear regression of CO_2 mixing ratio change over a 60 s interval beginning 1 min following chamber closure. This time delay was used to minimize any disturbance caused by chamber closure. Furthermore, we excluded measurements beyond the 60 s interval to minimize flux reduction resulting from an increase in chamber CO_2 mixing ratio. Five soil chambers were used during the growing season and two to three were used during winter.

A bole chamber was controlled and monitored using the chamber system described above. The bole chamber was constructed from clear flexible plastic (polyethylene) that enclosed a 0.47 m vertical section of the tree bole with a circumference of 0.70 m. The chamber was ventilated with a fan and a 30 cm long, 4 mm ID open ended tube allowed pressure equilibration with the atmosphere. During the sampling interval the chamber was closed and the CO_2 mixing ratio change was monitored over a 60 s interval.

2.3. Eddy covariance flux measurements

Wind velocity and temperature fluctuations were measured with a three-dimensional sonic anemometer-thermometer (model R3, Gill Instruments, Lymington, UK) mounted above the forest on a scaffold tower at a height of 39 m relative to the ground surface. CO_2 fluctuations were measured using a closed-path IRGA (model 6262, LI-COR Inc., Lincoln, NE, USA). The IRGA was located in a temperature-controlled enclosure and mounted on the canopy tower within 3 m of the sonic anemometer. A heated tube, 4 m in length, was connected to the IRGA, which sampled air from within 30 cm of the sonic anemometer. A diaphragm pump (model DOA-V191-AA, Gast Inc., Dayton, OH) pulled the air through the IRGA at a flow rate of 10 L min^{-1} . Half-hour block averaged CO_2 eddy fluxes (F_c) were computed from

$$F_c = \frac{\bar{\rho}_a}{M_a} \overline{w' s'_c} \quad (2)$$

where ρ_a is the density of dry air, M_a the molecular weight of dry air, w the vertical velocity, s_c the CO_2 mole mixing ratio, the primes indicate the differences

between instantaneous and mean values and the over bar indicates an averaging operation. $\overline{w's'_c}$ is the covariance of w and s_c . The averaging interval used was 30 min. Energy balance closure, based on daytime and nighttime half-hour values, was 88%. CO₂ fluxes were storage corrected using an 8-level CO₂ concentration profile system. Net ecosystem productivity (NEP) was computed from

$$\text{NEP} = -\text{NEE} = -(F_c + S_c) \quad (3)$$

where S_c is the rate of change in CO₂ storage in the air column extending from the forest floor to the sonic anemometer. Missing F_c observations accounted for 18% of the total half-hour flux measurements. Approximately 2% of the missing observations resulted from system calibration. The remaining missing data were caused by frost accretion on the sonic anemometer transducers and power failure (see Chen et al. (1999) for a detailed description of the EC system).

2.4. Ancillary measurements

Soil temperature was measured at depths of 2, 5, 10, 20, 50 and 100 cm using copper–constantan thermocouples. Volumetric liquid soil water content was measured at depths of 2.5, 7.5, 22.5, 45 and 75 cm using Campbell Scientific Inc. CS-615 soil water reflectometers. Bole temperature (T_b) was measured at a height of 3 m by inserting thermocouples 2 mm beneath the bark surface on the north and south sides. T_b was also monitored at a depth of 2 cm and at the center of the tree bole. Unless stated otherwise, the temporal variation of respiration was examined with respect to changes in soil temperature (T_s) and volumetric soil liquid water content (θ_s) measured at a depth of approximately 2.5 and 7.5 cm, respectively. Leaf area index (LAI) was measured using the LAI-2000 plant canopy analyzer, following Chen et al. (1997) and Kucharik et al. (1998).

2.5. Estimating annual net ecosystem exchange, respiration and photosynthesis

Annual NEE was obtained by gap-filling missing half-hour flux data and, as well, by replacing nighttime fluxes when turbulence was not fully developed (i.e. friction velocity (u_*) $< 0.35 \text{ m s}^{-1}$) (Barr et al.,

2002; Griffis et al., 2003). Approximately 44% of the nighttime data was replaced as a result of low u_* conditions. Missing flux data during the nighttime and non-growing season were filled using a respiration-temperature function obtained from the regression of nighttime NEE versus the 2 cm soil temperature for $u_* > 0.35 \text{ m s}^{-1}$. We define the growing season as 1 May 2001 to 1 October 2001, which corresponded to the period when leaves were present and net daytime CO₂ gain was observed. Missing daytime flux data from the growing season was filled using a light-response function computed using a 14-day moving window (see Griffis et al. (2003) for a detailed discussion of the gap-filling procedure and uncertainty in annual flux totals). Annual ecosystem respiration (R_E) was computed from the sum of the observed and gap-filled half-hourly nighttime values and the daytime estimate from the respiration-temperature function. P_g was computed from $P_g = \text{NEP} + R_E$.

3. Results

3.1. Forest climate and phenology

Climatic conditions during 2001 were warmer ($+1.3^\circ\text{C}$) and drier (-153 mm) than the 30-year (1971–2000) normal (0.4°C and 467 mm) recorded at Waskesiu Lake. The maximum and minimum recorded air temperature, measured at a height of 39 m, was 30.2 and -30.6°C , respectively. Soil temperature at a depth of 2 cm averaged 4.6°C . Although precipitation events were relatively frequent, their magnitude was significantly reduced during May and July. The total precipitation in these months was approximately 90 mm below normal. This resulted in a significant decrease in the August–September volumetric soil water content, which had not been observed previously at this site during CO₂ flux measurements (Fig. 1). The relatively warm spring period caused the second earliest leaf emergence date (30 April 2001) recorded at SOA since CO₂ flux measurements began in 1994. Total leaf area index (understory + overstory) reached a maximum value of $5.1 \text{ m}^2 \text{ m}^{-2}$ on 9 June. The maximum aspen and hazelnut LAI was 2.8 and $2.3 \text{ m}^2 \text{ m}^{-2}$, respectively. LAI was relatively constant following 9 June but decreased rapidly after 18 September.

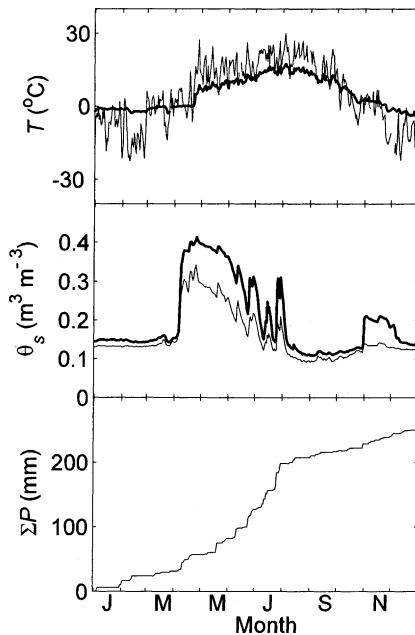


Fig. 1. Forest climate at the southern old aspen site during 2001. Air temperature (T_a) was measured at the height of the sonic anemometer (33 m) (thin line); soil temperature (T_s) was measured at a depth of 2 cm (top panel) (thick line); soil water content was measured at a depth of 2.5 (thin line) and 7.5 cm (thick line) using time domain reflectometry (TDR) (middle panel). Cumulative precipitation was measured with a weighing gauge (bottom panel). Climatic conditions during 2001 were warmer (annual air temperature 1.3°C higher) and drier (annual precipitation 153 lower) than the 30-year normal.

3.2. Soil and ecosystem respiration

The seasonal variation in R_s (measured with chambers) and R_E (measured with EC) is shown in Fig. 2. Half-hour values of R_s reached a maximum of $15.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ during July when the mean T_s and θ_s was 18°C and $0.24 \text{ m}^3 \text{m}^{-3}$, respectively. Half-hour values of R_E reached approximately $15.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ during July and early August. During January and December half-hour values of R_s and R_E reached a maximum of about 1 and $2 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. During the growing season the half-hour to half-hour variation in R_s was typically $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ whereas the variation in nighttime R_E was often greater than $4 \mu\text{mol m}^{-2} \text{s}^{-1}$. Statistical correlation among the individual chamber observations was high ($r > 0.92$) indicating that the

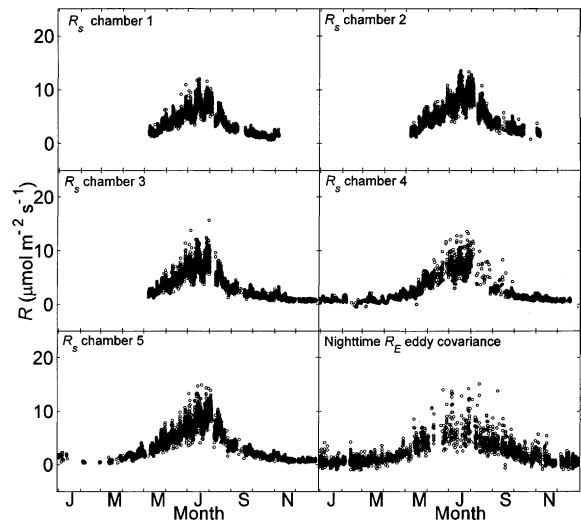


Fig. 2. Seasonal variation of soil and ecosystem respiration. Soil respiration (R_s) was measured every half-hour using an automated chamber system. Two chambers (4 and 5) were operated over the entire year. Nighttime ecosystem respiration (R_E) was measured every half-hour and is shown for conditions with $u_* > 0.35 \text{ m s}^{-1}$.

temporal variation at each location was controlled by the same environmental factors. The coefficient of spatial variation (CV) in R_s , estimated from the standard deviation divided by the average flux from all half-hour soil chamber observations, was 18% indicating that the spatial variability in the fluxes was relatively similar.

The annual average nighttime R_s and R_E (Fig. 3) were 1.1 ± 0.66 and $0.85 \pm 0.64 \text{ g C m}^{-2}$ per day, respectively. The day-to-day and seasonal variations in nighttime R_s and R_E were strongly correlated, and the July averages were 2.1 ± 0.47 and $2.1 \pm 0.91 \text{ g C m}^{-2}$ per day, respectively. The daytime average NEE (negative values indicate net CO_2 gain, i.e. positive NEP), measured with EC, and R_s is also shown in Fig. 3. During the non-growing season the agreement between NEE (i.e. R_E) and R_s was good. The average December nighttime R_s and R_E was 0.50 ± 0.04 and $0.30 \pm 0.12 \text{ g C m}^{-2}$ per day, respectively. From DOY 346 (12 December 2001) to DOY 350 (16 December 2002) air temperature increased from -25 to 2°C causing only a small increase in R_s and R_E . The daytime growing season (1 May–1 October) R_s reached a maximum of 3.4 g C m^{-2} per day and averaged 1.6 g C m^{-2} per day. Average growing season daytime NEP was

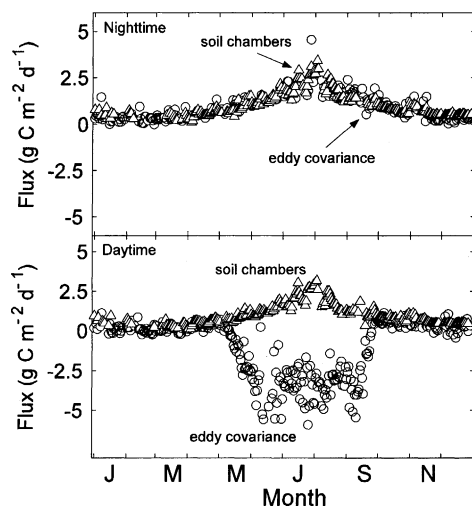


Fig. 3. Comparison of nighttime (top panel) and daytime (bottom panel) fluxes measured with soil chambers and the eddy covariance system. Eddy covariance measurements are shown for $u_* > 0.35 \text{ m s}^{-1}$. Fluxes are shown for periods when there was a minimum of five acceptable observations. For daytime fluxes (bottom panel) the negative fluxes indicate periods when there was a net gain of CO_2 by the forest measured with the eddy covariance system.

$2.6 \pm 1.6 \text{ g C m}^{-2}$ per day while the maximum value was 5.9 g C m^{-2} per day. The strong reduction in summertime θ_s , resulted in a pronounced decrease in R_E and R_s during mid to late August into September. During this extreme dry period ($\theta_s = 0.10 \text{ m}^3 \text{ m}^{-3}$ at 2.5 cm and $\theta_s = 0.12 \text{ m}^3 \text{ m}^{-3}$ at a depth of 7.5 cm) daytime NEP remained relatively large (Fig. 3). These data suggest that R_E showed greater sensitivity to θ_s than photosynthesis (Barr et al., 2004b). The monthly sums of R_s , R_E , and NEE, based on the average 24 h fluxes, are shown in Table 1 and illustrate that the greatest respiratory CO_2 losses occurred during July and that the greatest net CO_2 gain occurred during June. In general, there was a strong correlation ($r^2 = 0.74$) between the average nighttime R_s and R_E (Fig. 4) indicating that the chamber and EC system capture similar seasonal dynamics. We note, however, that the average of the nighttime chamber measurements of R_s was approximately 29% greater than the average R_E values measured with EC. Fig. 4 illustrates some non-linearity with a tendency for larger chamber fluxes to be observed at the low and high ends of the range.

Table 1

Monthly totals (g C m^{-2}) of ecosystem respiration (R_E), soil respiration (R_s) and net ecosystem CO_2 exchange (NEE) at the southern boreal aspen forest in 2001

Month	R_E	R_s	NEE
January	21.8	28.1	16.4
February	18.5	22.3	12.1
March	25.4	28.9	17.7
April	42.0	41.0	30.3
May	104.8	87.1	−18.9
June	159.4	151.7	−168.7
July	218.0	230.1	−145.7
August	175.2	178.9	−97.7
September	93.7	85.4	−29.7
October	46.1	46.5	39.0
November	37.0	38.4	29.9
December	19.0	23.5	14.9
Total	961	962	−300

R_E and NEE were measured with the eddy covariance approach. Nighttime half-hour periods with $u_* < 0.35 \text{ m s}^{-1}$ were gap filled using a respiration-temperature function for nighttime and non-growing season periods. R_E values derived from the temperature regression function were adjusted according to the soil water content residual analysis shown in Fig. 7. A 14-day moving window light-response function was used to fill missing data during daytime growing season conditions. R_s is based on the average of the individual chamber observations. Missing values were obtained from a function of R_s vs. soil temperature (2 cm depth) based on all available soil chamber data and adjusted according to the soil water content residual analysis shown in Fig. 7.

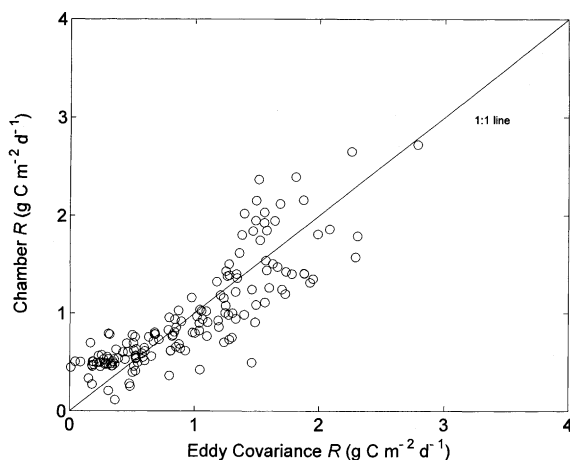


Fig. 4. Comparison of nighttime respiration measured with the automated soil chamber system and the eddy covariance technique. Chamber fluxes were averaged for all available soil chambers. The average of the soil chamber measurements (R_s) was approximately 29% greater than the eddy covariance estimate of ecosystem respiration (R_E).

3.3. Tree bole respiration

Tree bole respiration (R_b), expressed as a flux per ground surface area was scaled up according to the bark area estimate of the aspen forest, provided by Gower et al. (1997). R_b was small and moderately correlated ($r^2 = 0.49$) with the 2 mm tree bole temperature (T_b) at a height of 3 m. Average daytime and nighttime fluxes were 0.76 ± 0.30 and $0.61 \pm 0.22 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively during the growing period (Fig. 5). Non-growing season R_b was small, but persistent and averaged $0.28 \pm 0.39 \mu\text{mol m}^{-2} \text{s}^{-1}$. The average values of daytime and nighttime growing season T_b were 16.3 and 12.5 °C, respectively. Corresponding maximum values were 30.6 and 23.4 °C. Maximum values of R_b were observed during June and occurred before the maximum observed bole and air temperatures that were recorded in July—providing

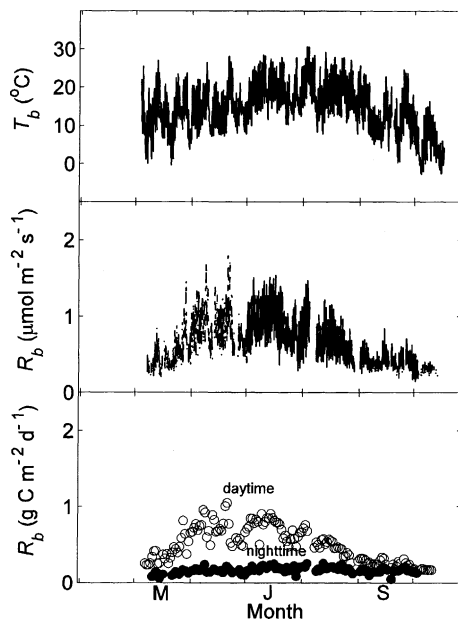


Fig. 5. Seasonal variation of half-hourly tree bole respiration (R_b) measured with an automated chamber (middle panel). The chamber was installed at a height of 1.3 m. The flux is expressed per ground area and scaled according to the bark area index of the aspen forest (Gower et al., 1997). Tree bole temperature (top panel) was measured at a depth of 2 mm below the bark. Tree bole respiration is shown for daytime (open symbols) and nighttime (closed symbols) for days with a minimum of five observations (bottom panel).

further evidence that autotrophic respiration is dependent on both temperature and phenological factors.

3.4. Temperature and soil water content controls on respiration

The relation of R_s , R_b and R_E to temperature is shown in Fig. 6. The raw and binned data are each shown to describe the influence of temperature on respiration. Temperature explained approximately 77, 49, and 60% of the variation in R_s , R_b , and R_E , respectively. There was a clear break-point in the relation between R_s and T_s at 6 °C. At $T_s > 6$ °C there was a rapid increase in R_s with a corresponding increase in variability. This observation was evident in both the aggregated chamber data and the individual chambers (data not shown). The 6 °C break-point may represent

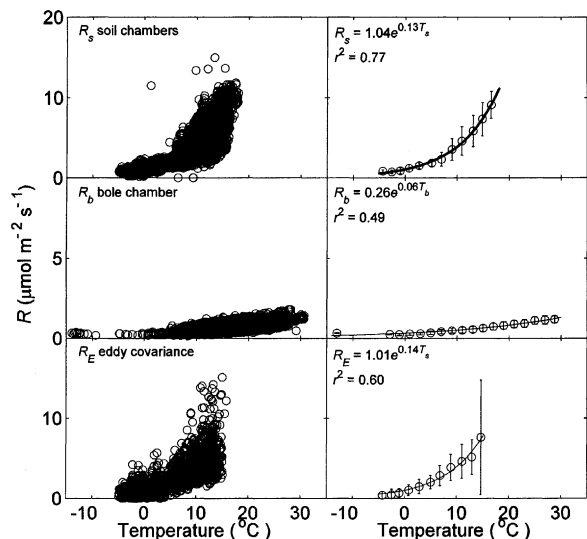


Fig. 6. Relation of soil (top panel), tree bole (middle panel) and ecosystem respiration (bottom panel) to temperature (soil temperature at 2 cm depth for soil and ecosystem respiration and 2 mm bole temperature at the 3 m height). Soil respiration (R_s) includes all available half-hour observations from five automated chambers. Tree bole respiration (R_b) was measured on a single tree at a height of 1.3 m. Ecosystem respiration (R_E) was measured using the eddy covariance technique at nighttime. Half-hour values of R_E are shown for $u_* > 0.35 \text{ m s}^{-1}$. Right-hand panels show functions using binned data for bin widths of 2 °C with a minimum bin size of $n = 10$. Error bars represent 1 S.D. The parameter values are shown for the binned relationships and the coefficient of determination (r^2) is reported for the non-binned data in the left-hand panels.

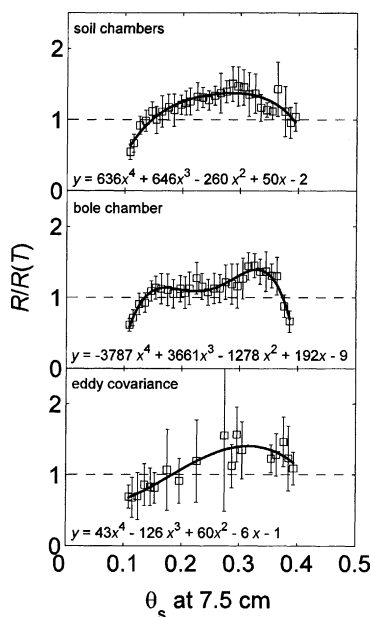


Fig. 7. Residual analysis showing the influence of soil water content measured at a depth of 7.5 cm on soil (R_s), tree bole (R_b) and ecosystem respiration (R_E). Residuals were obtained from the temperature functions shown in Fig. 7 as $R/R(T)$. Residuals were classed according to bin widths of $0.01 \text{ m}^3 \text{ m}^{-3}$ with a minimum bin size of $n = 10$. Error bars represent 1 S.D.

the transition from R_s dominated by heterotrophic activity to R_s controlled by heterotrophic and autotrophic activity, which have been shown to be strongly coupled (Högberg et al., 2001). For example, photosynthate production and root exudates provide a primary source of organic carbon for rapid utilization by microbes. In general, R_s dominated the shape of the R_E temperature response curve.

The cause of the increased variation in respiration can partially be explained by changes in θ_s . A residual analysis (Fig. 7), after accounting for the effects of temperature, showed that residual R_s (i.e., $R_s/R_s(T)$) was <1 for $0.15 > \theta_s > 0.38 \text{ m}^3 \text{ m}^{-3}$ and >1 for $0.15 < \theta_s < 0.38 \text{ m}^3 \text{ m}^{-3}$. Similar patterns were observed for the residuals of R_b and R_E . Residual R_b (i.e., $R_b/R_b(T)$) was >1 for $0.13 < \theta_s < 0.38 \text{ m}^3 \text{ m}^{-3}$. The residual values of R_E (i.e., $R_E/R_E(T)$) were consistent with the patterns for R_s and R_b but showed larger departures from unity and greater standard deviation. In this exceptionally dry year, respiration functions based only on temperature tended to cause an overestimate

of respiration at both low and high θ_s and underestimated respiration at moderate θ_s .

3.5. Phenological and photosynthetic controls on respiration

Changes in phenology and available photosynthetic substrates are expected to be important factors in determining the seasonal variation in R_E (Högberg et al., 2001). These factors, however, have been challenging to quantify because of their strong autocorrelation with the seasonal variation of temperature and volumetric soil water content. We examined changes in daytime R_s as a residual ($R_s/R_s(T_s, \theta_s)$) of light-saturated NEP (NEP_{\max}) and found a small increase in residual R_s ($R_s/R_s(T_s, \theta_s) = 0.015NEP_{\max} + 0.70$, $r^2 = 0.19$) as NEP_{\max} increased. The weak relationship is due in part to the strong influence of temperature on changes in phenology and photosynthesis. The residual analysis for R_b ($R_b/R_b(T_b, \theta_s)$) showed a slightly stronger ($R_b/R_b(T_b, \theta_s) = 0.026NEP_{\max} + 1.12$, $r^2 = 0.22$) dependence on NEP_{\max} . It is interesting to note that R_b showed the weakest correlation (Fig. 6) with temperature compared to R_s and R_E . Results from the residual analysis suggest that phenology and/or availability of carbon substrates must have a significant influence on R_b .

The sensitivity of daytime and nighttime R_s showed that there was no significant difference between the sensitivities (i.e., $Q_{10} = 3.5$) between the daytime and nighttime response to temperature. The annual Q_{10} of R_E was approximately 3.8 for T_s ranging from -4.2 to 14.6°C . The Q_{10} for R_b was significantly smaller ($Q_{10} = 1.8$) than the values for R_s and R_E for a temperature range of -18.9 to 28.8°C and was approximately 20% larger than values reported by Lavigne and Ryan (1997) for SOA. Using the same temperature range for R_E (i.e. $T_b = -4.2$ to 14.6°C), the Q_{10} of R_b was 1.8 and significantly smaller than the Q_{10} for R_s and R_E . The Q_{10} of R_b did not vary significantly between day or night illustrating that the daytime–nighttime R_b difference was driven by changes in T_b . The Q_{10} of R_b , however, showed a consistently decreasing trend ($Q_{10} = -0.0021\text{DOY} + 1.9$, $r^2 = 0.58$) from the timing of leaf emergence to leaf senescence, which was independent of the range of T_b . Lavigne and Ryan (1997) observed a decrease in the Q_{10} of R_b

from about 1.3 during peak growing season to about 1.0 after senescence. Tjoelker et al. (2001) demonstrated that the Q_{10} of a variety of boreal tree species, including *P. tremuloides*, decreased with increasing temperature. These results illustrate that time of season (phenology) can also have an important influence on the Q_{10} value, which has important modeling implications.

3.6. Partitioning and constraining ecosystem respiration

Chamber measurements and biotic functions were used to scale up from soil, bole and leaf to the canopy to obtain an independent estimate for comparison with the EC derived annual respiration (R_E). Respiration-temperature functions were used to replace missing values. To account for the effects of soil water content, each respiration-temperature function was corrected according to the residual analysis shown in Fig. 7. The parameters and annual totals for each component are presented in Table 2. Scaled estimates of R_s , R_b , and leaf respiration (R_l) produced an annual total carbon loss of 1315 g C m^{-2} per year.

The corresponding R_E estimate (from EC measurements) was $961 (1092) \text{ g C m}^{-2}$, which was 37 (20)% less than the scaled value (bracketed terms indicate the EC values after they were corrected for lack of energy balance closure). Annual R_s was 962 g C m^{-2} and was about 160 g C m^{-2} per year greater than the long-term (49-year) modeled estimate reported by Russell and Voroney (1998) for SOA. Annual bole respiration was 155 g C m^{-2} . R_l was estimated as 198 g C m^{-2} per year using parameters obtained from Ryan et al. (1997) (Table 2).

Uncertainty in scaling the chamber fluxes was attributed to spatial variation, and a coefficient of spatial variation ($CV = 20\%$) was used to estimate the potential error for each of the components (Table 2). A random error of 25% was assigned to the EC respiration estimate (see Morgenstern et al. (in press) for a similar treatment of the maximum random error). The potential random error resulting from the chamber scaling procedure produced an uncertainty range of $1052\text{--}1578 \text{ g C m}^{-2}$ per year. The annual uncertainty of R_E using the EC approach ranged from 721 to 1201 g C m^{-2} per year. Therefore, the annual estimate of R_E and the scaled respiration value were

Table 2
Scaling up ecosystem respiration using an automated chamber system at the southern boreal aspen forest in 2001

Component	Function parameters							Annual R (g C m^{-2} per year)
	p_1	p_2	m_l	r_B	T_B	Q_{10}	Random error (%) ^a	
Soil ^b	1.04	0.13				3.0	20	962 ± 192
Leaf ^c			5.8	0.51	10	2.1	20	198 ± 40
Bole ^b	0.26	0.06				1.8	20	155 ± 31
Total								1315 ± 263
Ecosystem ^d	1.01	0.14				3.8	25	961 ± 240

Annual totals of soil, bole and ecosystem respiration are based on measurements and gap-filling procedures.

^a The cumulative random error of the scaled chamber and eddy covariance fluxes was assessed following the method of Wesely and Hart (1985) and Morgenstern et al. (in press). The random error terms for the chamber fluxes were assigned a value of 20%, which is consistent with the coefficient of variation observed for the soil chamber fluxes. The random error for the eddy covariance fluxes was assigned a value of 25%. The cumulative annual error (ξ) for each chamber component and the eddy covariance estimate of ecosystem respiration was obtained from, $\xi = \Delta \sqrt{\sum_i (F(i))^2}$, where Δ is the random error term and $F(i)$ is the half-hour flux.

^b Soil and bole respiration measured using automatic chambers at SOA during 2001, $R_s = p_1 \exp(p_2 T_s)$ and $R_b = p_1 \exp(p_2 T_b)$, respectively, where T_s is the soil temperature at a depth of 2 cm and T_b was measured approximately 2 mm below the bark on the south and north facing sides of the tree bole at a height of 3 m.

^c Leaf respiration estimated using a closed chamber system from Ryan et al. (1997), where $R_l = m_l r_B Q_{10}^{(T_l - T_B)/10}$, where R_l is the respiration rate from the leaf tissue, m_l the leaf area index ($\text{m}^2 \text{ m}^{-2}$), r_B the mean tissue respiration rate for leaves ($\mu\text{mol m}^{-2} \text{ s}^{-1}$), T_B the base temperature, and Q_{10} the change in respiration for a 10°C change in temperature and T_l the leaf temperature. The soil, tree bole and ecosystem respiration functions were scaled by the residual functions shown in Fig. 7 to account for the effects of soil water content.

^d From eddy covariance using the nighttime $R(T_s)$ relation for $u_* > 0.35 \text{ m s}^{-1}$.

within the uncertainty of both methods. Consistent with other studies (Goulden et al., 1996; Lavigne et al., 1997; Law et al., 2000; Drewitt et al., 2002), however, the scaled approach provided a larger estimate of R_E . Russell and Voroney (1998) examined the spatial variation of R_s using a small portable dynamic chamber (10 cm diameter) and concluded that approximately 40 chambers would be required to estimate within 10% of the mean flux at the 95% probability level. The larger chamber surface area used in this study, however, has reduced the observed spatial variation as evidenced by the lower CV in R_s .

R_s was partitioned into root-mycorrhizal respiration (R_r) and heterotrophic microbial respiration (R_h) to obtain estimates of autotrophic respiration (R_a) and net primary production (NPP). Estimates of R_r vary from 10 to 90% of R_s , depending on the partitioning methodology and the ecosystem type (Hanson et al., 2000). For example, Högberg et al. (2001) concluded that R_r was a 54% fraction of R_s based on a tree-girdling experiment in a boreal pine forest. Bond-Lamberty et al. (in press) recently examined the relationship between heterotrophic and autotrophic components of soil respiration for a broad range of forests. They studied published data from 53 different forest stands (including SOA) using several partitioning methods (root exclusion, comparison of unburned with recently burned stands, manipulation of root photosynthate supply, root extraction, isotope labeling and mass balance techniques) and proposed the general equation ($R_r^{0.5} = -7.94 + 0.94R_s^{0.5}$, $r^2 = 0.87$, $P < 0.001$) to partition R_s into R_r . From this equation we estimated that R_r accounted for 47% of R_s at SOA in 2001. Long-term root exclusion and soil chamber experiments are currently being conducted at other BERMS sites to examine the interannual and seasonal variation of this important belowground partitioning. Using the above equation we calculated heterotrophic microbial respiration (R_h) and R_r as 510 and 452 g C m⁻² per year, respectively (Table 3).

The ratio of NPP/ P_g was used to further evaluate the quality of the annual estimate of ecosystem respiration obtained using the EC approach. For example, Gifford (1994) and Waring et al. (1998) have shown that NPP/ P_g is relatively conservative for a broad range of ecosystems. Gifford (1994) found that the NPP/ P_g ratio was about 0.6 while Waring et al. (1998) obtained a ratio of about 0.47. The NPP/ P_g ratio can provide an

Table 3

Estimating net primary production and the ratio of NPP to gross photosynthesis from chamber and eddy covariance measurements for 2001

C balance component or ratio	g C m ⁻² per year
R_s	962
R_b	155
R_l	198
R_E	1315 (961)
R_r^a	452
R_h	510 (375 ^b)
R_a	805 (586 ^b)
R_a/R_E	0.61
NEP	300
P_g	1615 (1261)
NPP	810 (675)
NPP/ P_g	0.50 (0.54)

Bracketed terms are estimates based on eddy covariance measurements, NPP was calculated as NPP = NEP + R_h .

^a Using the 0.47 fraction of soil respiration that is attributed to root respiration of chamber R_s (Bond-Lamberty et al., in press).

^b Values were obtained by scaling the eddy covariance estimate of R_E by the chamber partitioning R_a/R_E ratio.

independent diagnostic parameter for constraining the annual EC respiration estimate (see Baldocchi et al. (1997) and Falge et al. (2002)).

Here we estimated NPP/ P_g ratios based on chamber and EC observations to identify potential problems with the EC carbon budget. The assumption is made that the uncertainty in the total annual ecosystem respiration estimate from the chambers is potentially large due to spatial variation, but that the relative contribution from ecosystem components is well constrained. For example, we have a high degree of confidence that R_s is the major component of R_E and that R_b and R_l are relatively small based on annual chamber observations. It follows, therefore, that the total R_a ($R_r + R_b + R_l$) estimated from the chamber scaling is 805 g C m⁻² per year, which represents 61% of the total chamber respiration. This chamber estimate of R_a is approximately 35% larger than that reported by Ryan et al. (1997) for SOA who obtained a value of 600 g C m⁻² per year.

NEE at SOA has been shown to be more similar to temperate deciduous forests than boreal (Barr et al., 2002). In 2001 NEP (i.e., -NEE) was approximately 300 g C m⁻² per year (Barr et al., 2004a) and ranked as the largest CO₂ sink year in the SOA flux record. The annual sum of P_g was 1261 g C m⁻², estimated from ($P_g = NEP + R_E = 300 + 961$) based on the EC data

(see Table 3). P_g was 17 g C m^{-2} per year lower than the average of the estimates made at SOA over the last 6 years (1994, 1996–2001) using EC fluxes and was not significantly different when considering the errors (Black et al., 2000; Barr et al., 2002; Griffis et al., 2003). In order to constrain the EC respiration estimate we obtained NPP as follows. First, we assumed that the relative contribution of ecosystem components to total respiration was well defined based on the chamber observations. The EC estimate of R_E , which provides better spatial representation, was then partitioned into R_a and R_h based on the chamber partitioning (i.e. R_a accounted for 61% of the total chamber respiration). Therefore, EC estimates of R_a and R_h were 586 and 375 g C m^{-2} per year, respectively. NPP was then calculated from $\text{NPP} = \text{NEP} + R_h = 675 \text{ g C m}^{-2}$ per year (Table 3).

The NPP estimate of 675 g C m^{-2} per year was nearly 2-fold greater than the value obtained by Gower et al. (1997) using biometric techniques at SOA, but was in better agreement with estimates for broad-leaf deciduous forests (Waring and Schlesinger, 1985) and boreal evergreen forests (Schulze, 1982). The NPP/P_g ratio was 0.54, which is between the ratios of Gifford and Waring et al. (Fig. 8). The ratio was similar to that presented by Falge et al. (2002) for temperate evergreen conifers and broad-leaf forests (0.51) and boreal systems (0.49–0.52) and was approaching the upper limit of the values presented by Waring et al. (1998) for a large variety of ecosystems. We recognize that the NPP/P_g ratio should vary interannually depending on how climate influences the ratio of R_a to P_g .

Fig. 8 illustrates the sensitivity of NPP/P_g to uncertainties in R_E and the ratio of R_a to R_E . This

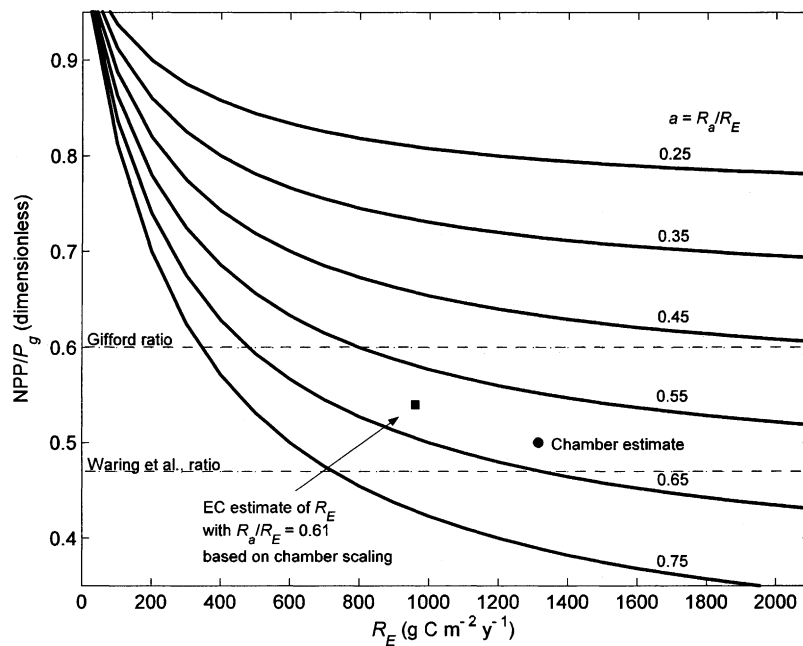


Fig. 8. Constraining the eddy covariance (EC) estimate of annual ecosystem respiration and net ecosystem production. Dashed horizontal lines indicate the published values of the “conservative” ratio NPP/P_g for a broad variety of ecosystems as reported by Gifford (1994) and Waring et al. (1998). Dark solid lines illustrate the sensitivity of NPP/P_g to the partitioning of ecosystem respiration (R_E) into autotrophic (R_a) and heterotrophic (R_h) respiration. These curves are given by $\text{NPP}/P_g = 1 - a/(1 + \text{NEP}/R_E)$ where $a = R_a/R_E$ (number next to each dark solid line). The calculations have been done using $\text{NEP} = 300 \text{ g C m}^{-2}$ per year (from Table 1). The square symbol shows the EC NPP/P_g ratio for SOA 2001. The circle shows the estimate based on the total chamber respiration (see Table 3 for analysis). The chamber scaling procedure combined with the annual EC estimate of R_E produced NPP/P_g ratios that were consistent with other independent studies, supporting that the eddy covariance budget for NEP , R_E and P_g is robust. Note that the derivatives, $(d\text{NPP}/P_g)/(dR_E/R_E) = (-aR_E\text{NEP})/(R_E + \text{NEP})^2$ and $(d\text{NPP}/P_g)/(d\text{NEP}/\text{NEP}) = (aR_E\text{NEP})/(R_E + \text{NEP})^2$, can be used to examine the sensitivity of the NPP/P_g ratio to the uncertainty in NEP and R_E directly. Given $a = 0.61$, $\text{NEP} = 300 \text{ g C m}^{-2}$ per year and $R_E = 961 \text{ g C m}^{-2}$ per year, the NPP/P_g ratio would vary $\pm 3\%$ for an uncertainty in either R_E or NEP of about $\pm 30\%$.

analysis shows that NPP/P_g values at SOA are likely within the range observed by Gifford and Waring et al., for $55 < R_a/R_E < 65\%$ for R_E ranging from 800 to 1400 g C m^{-2} per year. Thus, this analysis indicates that the annual sum of chamber respiration (1315 g C m^{-2} per year) with 61% attributed to R_a would also result in an NPP/P_g ratio within the observed range of Gifford and Waring et al. Therefore, this relatively good agreement, where ratios were obtained by combining chamber and EC techniques and compared with published values of NPP/P_g , suggests that: (1) the relative rates of respiration from ecosystem components are adequately measured using the automated chamber system; (2) the annual EC estimate of R_E and its partitioning into R_a and R_h is realistic—otherwise, we would expect NPP/P_g ratios to lie outside the expected range illustrated in Fig. 8; (3) NEP obtained using gap-filling procedures is consistent with the NPP/P_g ratios. We note, however, that the sensitivity of NPP/P_g to R_E is relatively low over the range of typical annual estimates of R_E and R_a for forests. These conclusions are also specific to our NEP value of 300 g C m^{-2} per year and would need to be re-evaluated for other cases. Furthermore, our conclusions are sensitive to our original assumption that R_r is 47% of R_s .

4. Discussion

4.1. Temporal variation of respiration

One of the strengths of the present study is the continuous and independent measurements of chamber and eddy covariance respiration over an annual cycle. The strong temporal resolution provides a better opportunity for quantifying the seasonal dynamics of respiration from ecosystem components. To date, the predominant control on soil, tree bole, and ecosystem respiration of this forest has been temperature with volumetric soil water content explaining only a small portion of the seasonal variation in respiration. Similar findings have been reported by other investigators for a broad range of ecosystems (Baldocchi et al., 1997; Russell and Voroney, 1998; Law et al., 2001; Lee et al., 1999; Griffis et al., 2000a; Drewitt et al., 2002; Flanagan et al., 2002). During the unprecedented drought period of August and September 2001,

soil and ecosystem respiration decreased appreciably while net ecosystem CO_2 sequestration was relatively large. Volumetric soil water content at extremely low values, less than $0.15 \text{ m}^3 \text{ m}^{-3}$, resulted in a substantial decrease in respiration. The relatively large CO_2 gain during these hot and dry conditions is a surprising result, illustrating for the first time that respiration can have greater sensitivity to climate than photosynthesis in this deciduous forest. Annual R_E was 961 g C m^{-2} per year and was on average substantially lower (171 g C m^{-2} per year) than the previous 6 years (Black et al., 2000; Barr et al., 2002; Griffis et al., 2003). Based on the long-term annual NEE record at SOA, it appears that net CO_2 gain can increase by increasing growing season length through a phenological response (timing of leaf emergence and senescence) (Black et al., 2000) and through the reduction of respiration in response to drought. The latter effect is likely to be a transient condition. Ecosystem respiration is expected to increase as the soils become rehydrated. Furthermore, persistent drought should reduce photosynthetic rates in the long-term as soil water becomes depleted in the rooting zone. These longer term drought effects are discussed in greater detail by Barr et al. (2004b) and Kljun et al. (2004).

Isolating the effect of phenological changes on respiration remains a challenging problem and not easily addressed with the measurement techniques used in this study. Residual analysis showed that R_s and R_b each increased with respect to light-saturated NEP. Temperature-dependent respiration functions capture changes resulting from maintenance and growth processes. The similar Q_{10} values observed for daytime and nighttime R_s and R_b suggests that respiration is not limited at night by reductions in photosynthetic products. Furthermore, the similarity in Q_{10} values confirms that the differences between daytime and nighttime respiration is largely driven by temperature and not changes in substrate availability. The linear decrease in tree bole respiration Q_{10} values from leaf emergence to leaf senescence suggests that temperature sensitivity is dependent on growth/phenological phase and may indicate a change in the ratio of maintenance to growth respiration.

R_E increased rapidly following leaf emergence (30 April 2001) and reached maximum values, $\sim 5 \text{ g C m}^{-2}$ per day at the end of July and correlated with warm soil temperatures and high photo-

synthetic rates. Summer season (1 May–1 October) R_E accounted for 751 g C m^{-2} and represented 78 and 60% of annual R_E and P_g , respectively, with the majority attributed to R_s . Non-growing season R_E accounted for 210 g C m^{-2} and represented only 22 and 17% of annual R_E and P_g , respectively. The function parameter values and Q_{10} defining R_E in 2001 were significantly smaller than values reported for SOA in 2000 (Griffis et al., 2003). The impact of drought on R_E can therefore cause a significant change in functional parameter values. These values ultimately need to be predicted from environmental conditions in climate-carbon models to avoid large biases. Continuous long-term CO_2 flux measurements are required, therefore, in order to bracket extreme environmental conditions so that models can be better parameterized.

R_E represented approximately 76% of P_g . This fraction is characteristic of temperate forests (Falge et al., 2002), whereas, boreal evergreen forests typically show relatively large R_E/P_g ratios >85% (Falge et al., 2002; Griffis et al., 2003). From 1994 to 2001, the R_E/P_g ratio at SOA averaged 0.87 with large deviations occurring in 1998 (i.e. 0.80) and 2001 (i.e. 0.76). We hypothesize that these deviations were related to an uncharacteristically large annual P_g in 1998 as a result of El Niño and early leaf emergence. In the latter case, however, R_E was substantially reduced and we hypothesize that it was R_h that decreased because of limiting soil water content. The NPP/P_g ratio, therefore, may vary considerably under extreme climatic conditions. For example, if R_h increased relative to R_a the NPP/P_g ratio would increase (see Fig. 8).

4.2. Constraining ecosystem respiration

The use of chambers to constrain respiration requires that the spatial variability in ecosystem components be well represented by relatively few chambers. The number of chambers used in any ecosystem study will be a limitation. Geostatistical techniques, such as semivariance analyses, have indicated a natural spatial scale or “patchiness” of approximately 1–10 cm for microbial biomass, as observed by Morris (1999) in an Ohio hardwood forest. Other soil variables, including pH, soil water content, and organic carbon content, showed autocorrelation at length scales less

than 1 m. Nunan et al. (2002) demonstrated that the spatial variation of microbes in topsoil and subsoil was distinct in an arable field soil and was correlated with variation in nutrients and hydraulic conductivity. A semivariance analysis showed that 100 and 46% of the microbial spatial variation in the topsoil and subsoil, respectively, occurred at scales <15 cm. Rayment and Jarvis (2000) argued that heterogeneity in soil respiration rates at a black spruce site in northern Saskatchewan, Canada increased only marginally beyond a length scale of about 1 m. The relatively large estimate of respiration, obtained from the scaling procedure in this study, therefore, is not likely a consequence of inadequate spatial coverage because the chamber dimensions and distance between chambers should adequately capture the characteristic spatial scale of the factors influencing soil respiration.

Reconciling the differences between EC and scaled chamber respiration estimates in forest ecosystems remains a difficult challenge. In many cases, chamber experiments have resulted in larger respiration estimates than EC approaches. This remains true after accounting for weak turbulent conditions (u_* correction) and energy balance closure. It should be emphasized that errors associated with making EC measurements work toward decreasing the flux magnitude (Massman and Lee, 2002). We highlight the observation that applying a correction for lack of energy balance closure reduced the difference between the EC and chamber based estimate of ecosystem respiration from 37 to 20%. A number of studies have reported significantly larger chamber respiration estimates than EC budgets (Goulden et al., 1996; Lavigne et al., 1997; Law et al., 2000; Drewitt et al., 2002) while others have shown good agreement for short-term comparisons (Law et al., 2001; Wallin et al., 2001; Griffis et al., 2000b). We are not aware of any studies indicating that chambers underestimate EC by a similar magnitude for forests.

The standard deviation of nighttime EC respiration was significantly larger than that obtained from the chamber measurements for all seasons illustrating a smaller signal to noise ratio for the EC approach. Daytime and nighttime estimates of respiration based solely on EC measurements (Griffis et al., 2003) show strong similarity despite significant differences in flux footprint size. Landscape heterogeneity, therefore, is

not likely an important factor in explaining the disparity. Factors such as nocturnal subsidence (discussed by Lee (1998)) suggest that advection could be an important mechanism accounting for the differences observed.

Comparisons of carbon balances, obtained from the EC approach, have shown good agreement with biomass inventories (Barford et al., 2001; Curtis et al., 2002; Ehman et al., 2002). However, too few studies have made these types of comparisons and, furthermore, the agreement has the potential to vary considerably depending on individual site conditions. Our independent analysis using chamber, EC, and published values of NPP provided a test to examine bias in our annual respiration and its partitioning. We conclude that our NPP/P_g ratios are not significantly different from literature values based on biometric techniques. Constraining ecosystem respiration estimates remains a difficult challenge, however, EC and automated chamber networks provide a means to study the seasonal and interannual dynamics of carbon exchange, which is critical to understanding the processes and improving ecosystem models. Continuous monitoring on interannual timescales will provide an opportunity to help understand and predict changes in function parameters and improve our ability to model the interannual variability in R_E and photosynthesis. Continued research on partitioning is required to better constrain current estimates of R_E and to help provide a better understanding of the factors controlling component fluxes.

5. Conclusions

1. Seasonal variability of soil (R_s), tree bole (R_b) and ecosystem (R_E) respiration was mainly controlled by temperature. Photosynthesis and phenology had a small but discernible impact on the seasonal variation of respiration.
2. Interannual variability of R_E was greatly affected by changes in soil water content and decreased substantially from the previous 6 years as a result of drought conditions. The reduction in R_E caused a significant increase in annual CO_2 sequestration and resulted in the largest value in 7 years of EC measurements at SOA.
3. Response of respiration to drought resulted in a significant change in the values of the parameters in the respiration function for 2001 compared to previous years. The ratio of R_E to P_g was 0.76 and was the smallest value observed in the SOA CO_2 flux record.
4. Scaled up chamber respiration was approximately 37% larger than the eddy covariance estimate of ecosystem respiration. The exact cause of the disparity is unknown; however, both independent estimates are within the range of uncertainty of the methodologies. The NPP/P_g ratio of 0.54 was within the range of recently published values using biometric techniques and supports that the relative rates of respiration from ecosystem components is adequately measured using the automated chamber system and that the annual EC estimate of R_E and its partitioning into R_a and R_h is well constrained.
5. Whereas earlier studies found that net CO_2 gain at SOA was controlled by increased growing season length resulting from phenological response to warm springs and early snowmelt, the EC measurements in 2001, the seventh year of measurements in the long-term record, illustrate that net CO_2 sequestration is also controlled by decreased respiration in response to drought. The contribution of respiration to the interannual variation in NEE is only realized under extreme dry conditions and is likely to be a transient response.

Acknowledgements

Funding for this research has been provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) in the form of a 2-year Postdoctoral Fellowship (TJG) and an Operating Grant (TAB). Additional support has been provided by the Meteorological Service of Canada through a Contribution Agreement to the University of British Columbia. The authors acknowledge the technical assistance of Andrew Sauter and technical support from the Meteorological Service of Canada (MSC) who helped maintain the automated chamber system through bi-weekly site visits during the summer and cold winter at SOA.

References

- Baldocchi, D.D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, W., Oechel, W., Paw, K.T., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: a new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. *Bull. Am. Meteorol. Soc.* 82, 2415–2434.
- Baldocchi, D.D., Vogel, C.A., Hall, B., 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. *Agric. For. Meteorol.* 83, 147–170.
- Barford, C.C., Wofsy, S.C., Goulden, M.L., Munger, J.W., Pyle, E.H., Urbanski, S.P., Hutyyra, L., Saleska, S.R., Fitzjarrald, D., Moore, K., 2001. Factors controlling long- and short-term sequestration of atmospheric CO₂ in a mid-latitude forest. *Nature* 294, 1688–1691.
- Barr, A.G., Griffis, T.G., Black, T.A., Lee, X., Staebler, R.M., Fuentes, J.D., Chen, Z., Morgenstern, K., 2002. Comparing the carbon budgets of boreal and temperate deciduous forest stands. *Can. J. For. Res.* 32, 813–822.
- Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., Nesic, Z., 2004a. The seasonal cycle of leaf area index above a boreal aspen-hazelnut forest in relation to net ecosystem productivity. Accepted by *Agric. For. Meteorol.*
- Barr, A.G., Black, T.A., Kljun, N., Morgenstern, K., Griffis, T.J., Hogg, E.H., 2004b. Climatic controls on the carbon and water budgets of a boreal aspen forest, 1994–2003. *Global Change Biology* in preparation.
- Black, T.A., Ben Hartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nexic, Z., Lee, X., Chen, S.G., Staebler, R., Novak, M.D., 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Glob. Change Biol.* 2, 219–229.
- Black, T.A., Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nesic, Z., Hogg, E.H., Neumann, H.H., Yang, P.C., 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophys. Res. Lett.* 27, 1271–1274.
- Bond-Lamberty, B., Wang, C., Gower, S.T., in press. A global relationship between the heterotrophic and autotrophic components of soil respiration. *Glob. Change Biol.*
- Chen, W.J., Black, T.A., Yang, P.C., Barr, A.B., Neumann, H.H., Nesic, Z., Blanken, P.D., Novak, M.D., Eley, J., Ketler, R.J., Cuenca, R., 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Glob. Change Biol.* 5, 41–53.
- Chen, J.M., Blanken, P.D., Black, T.A., Guilbeault, M., Chen, S., 1997. Radiation regime and canopy architecture in a boreal aspen forest. *Agric. For. Meteorol.* 86, 107–125.
- Curtis, P.S.P.J., Hanson, P., Bolstad, C., Barford, J.C., Randolph, H.P., Schmid, Wilson, K.B., 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agric. For. Meteorol.* 113, 3–19.
- Drewitt, G.B., Black, T.A., Nesic, Z., Humphreys, E.R., Jork, E.M., Swanson, R., Ethier, J., Griffis, T.J., Morgenstern, K., 2002. Measuring forest floor CO₂ fluxes in a Douglas-fir forest. *Agric. For. Meteorol.* 110, 299–317.
- Ehman, J.L., Schmid, H.P., Grimmer, C.S.B., Randolph, J.C., Hanson, P.J., Wayson, C.A., Cropley, F.D., 2002. An initial intercomparison of micrometeorological and ecological inventory estimates of carbon exchange in a mid-latitude deciduous forest. *Glob. Change Biol.* 8, 575–589.
- Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A., Granier, A., Guomundsson, J., Hollinger, D., Kowalski, A.S., Katul, G., Law, B.E., Malhi, Y., Meyers, T., Monson, R.K., Munger, J.W., Oechel, W., Paw, U.K.-T., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., Wofsy, S., 2002. Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agric. For. Meteorol.* 113, 53–74.
- Flanagan, L.B., Wever, L.A., Carlson, P.J., 2002. Seasonal and interannual variation in carbon dioxide exchange and carbon balance in a northern temperate grassland. *Glob. Change Biol.* 8, 599–615.
- Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404, 858–861.
- Gifford, R.M., 1994. The global carbon cycle: a viewpoint on the missing sink. *Aust. J. Plant Physiol.* 21, 1–15.
- Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., Wofsy, S.C., 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Glob. Change Biol.* 2, 169–182.
- Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., Stow, T.K., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *J. Geophys. Res.* 102, 29029–29041.
- Grace, J., Rayment, M., 2000. Respiration in the balance. *Nature* 404, 809–820.
- Griffis, T.J., Rouse, W.R., Waddington, J.M., 2000a. Interannual variability in net ecosystem CO₂ exchange at a subarctic fen. *Glob. Biogeochem. Cycl.* 14, 1109–1121.
- Griffis, T.J., Rouse, W.R., Waddington, J.M., 2000b. Scaling net ecosystem CO₂ exchange from the community to landscape-level at a subarctic fen. *Glob. Change Biol.* 6, 459–473.
- Griffis, T.J., Black, T.A., Morgenstern, K., Barr, A., Nesic, Z., Drewitt, G., Gaumont-Guay, D., McCaughey, H., 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. *Agric. For. Meteorol.* 117, 53–71.
- Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* 48, 115–146.
- Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411, 789–792.

- Janssens, I.A., Lankreijer, H., Matteucci, G., Kowalski, A.S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grünwald, T., Montagnani, L., Dore, S., Rebmann, C., Moors, E.J., Grelle, A., Rannik, Ü., Morgenstern, K., Oltchev, S., Clement, R., Gundersson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N.O., Vesala, T., Granier, A., Schulze, E.D., Lindroth, A., Dolman, A.J., Jarvis, P.G., Ceulemans, R., Valentini, R., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Glob. Change Biol.* 7, 269–278.
- Jarvis, P.G., Dolman, A.J., Schulze, E.D., Matteucci, G., Kowalski, A.S., Ceulemans, R., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Gundersson, J., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Valentini, R., 2001. Carbon balance gradient in European forests: should we doubt 'surprising' results? A reply to Piovesan and Adams. *J. Veg. Sci.* 12, 145–150.
- Kljun, N., Black, T.A., Barr, A.G., Gaumont-Guay, D., Griffis, T.J., Morgenstern, K., McCaughey, J.H., Nesic, Z., 2004. Carbon uptake by three boreal forests in varying climate. *Glob. Change Biol.*, in preparation.
- Kucharik, C.J., Norman, J.M., Gower, S.T., 1998. Measurements of leaf orientation, light distribution and sunlit leaf area in a boreal aspen forest. *Agric. For. Meteorol.* 91, 127–148.
- Lavigne, M.B., Ryan, M.G., Anderson, D.E., Baldocchi, D.D., Crill, P.M., Fitzjarrald, D.R., Goulden, M.L., Gower, S.T., Massheder, J.M., McCaughey, J.H., Rayment, M., Striegl, R.G., 1997. Comparing nocturnal eddy covariance measurements to the estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites. *J. Geophys. Res.* 102, 28977–28985.
- Lavigne, M.B., Ryan, M.G., 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiol.* 17, 543–551.
- Law, B.E., Williams, M., Anthoni, P.M., Baldocchi, D.D., Unsworth, M.H., 2000. Measuring and modeling seasonal variation of carbon dioxide and water vapour exchange of *Pinus ponderosa* forest subject to soil water deficit. *Glob. Change Biol.* 6, 613–630.
- Law, B.E., Kelliher, F.M., Baldocchi, D.D., Anthoni, P.M., Irvine, J., Moore, D., Van Tuyl, S., 2001. Spatial and temporal variation in respiration in a young *ponderosa* pine forest during a summer drought. *Agric. For. Meteorol.* 110, 27–43.
- Lee, X., 1998. On micrometeorological observations of surface-air exchange over tall vegetation. *Agric. For. Meteorol.* 91, 39–49.
- Lee, X., Fuentes, J.D., Staebler, R.M., Neumann, H.H., 1999. Long-term observation of the atmospheric exchange of CO₂ with a temperate deciduous forest. *J. Geophys. Res.* 104, 15975–15984.
- Mahrt, L., 1998. Flux sampling errors for aircraft and towers. *J. Atmos. Oceanic Technol.* 15, 416–429.
- Massman, W.J., Lee, X., 2002. Eddy covariance flux corrections and uncertainties in long-term studies of carbon and energy exchanges. *Agric. For. Meteorol.* 113, 121–144.
- Morgenstern, K., Black, T.A., Humphreys, E.R., Griffis, T.J., Cai, T., Drewitt, G.B., Gaumont-Guay, D., Nesic, Z., in press. Sensitivity and uncertainty of the carbon balance of a Pacific northwest Douglas-fir forest during an El Niño/La Niña cycle. *Agric. For. Meteorol.* 123, 201–219.
- Morris, S.J., 1999. Spatial distribution of fungal and bacterial biomass in southern Ohio hardwood forest soils: fine scale variability and microscale patterns. *Soil Biol. Biochem.* 31, 1375–1386.
- Nunan, N., Wu, K., Young, I.M., Crawford, J.W., Ritz, K., 2002. In situ spatial patterns of soil bacterial populations, mapped at multiple scales, in arable soil. *Microb. Ecol.* 44, 296–305.
- Piovesan, G., Adams, J.M., 2001. Carbon balance gradient in European forests: interpreting EUROFLUX. *J. Veg. Sci.* 11, 923–926.
- Raymond, M.B., Jarvis, P.G., 2000. Temporal and spatial variation of soil CO₂ efflux in a Canadian boreal forest. *Soil Biol. Biochem.* 32, 35–45.
- Russell, C.A., Voroney, R.P., 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. 1. Relationship to environmental variables and estimates of C respired. *Can. J. Soil Sci.* 78, 301–310.
- Ryan, M.G., Lavigne, M.B., Gower, S.T., 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *J. Geophys. Res.* 102, 28871–28883.
- Schulze, E.-D., 1982. Plant life forms as related to plant carbon, water and nutrient relations. In: Lange, O.L., Nobel, P.S., Osmond, C.B., Ziegler, H. (Eds.), *Encyclopedia of Plant Physiology, Physiological Plant Ecology, Water Relations and Photosynthetic Productivity*, vol. 12B. Springer, Berlin, pp. 615–676.
- Sellers, P.J., Hall, F.G., Kelly, R.D., Black, A., Baldocchi, D., Berry, J., Ryan, M., Ranson, K.J., Crill, P.M., Lettenmaier, D.P., Margolis, H., Cihlar, J., Newcomer, J., Fitzjarrald, D., Jarvis, P.G., Gower, S.T., Halliwell, D., Williams, D., Goodison, B., Wickland, D.E., Guertin, F.E., 1997. BOREAS in 1997: experiment overview, scientific results and future directions. *J. Geophys. Res.* 102, 28731–28770.
- Tjoelker, M.G., Oleksyn, J., Reich, P., 2001. Modeling respiration of vegetation: evidence for a general temperature-dependent Q₁₀. *Glob. Change Biol.* 7, 223–230.
- Valentini, R., Matteucci, G., Dolman, A.J., Schulze, E.D., Rebmann, C., Moors, E.J., Granier, A., Gross, P., Jensen, N.O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grünwald, T., Aubinet, M., Ceulemans, R., Kowalski, A.S., Vesala, T., Rannik, Ü., Berbigier, P., Loustau, D., Gundersson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff, J., Montagnani, L., Minerbi, S., Jarvis, P.G., 2000. Respiration as the main determinant of carbon balance in European forests. *Nature* 404, 861–865.
- Wallin, G., Linder, S., Lindroth, A., Rantfors, M., Flemberg, S., Grelle, A., 2001. Carbon dioxide exchange in Norway spruce at the shoot, tree and ecosystem scale. *Tree Physiol.* 21, 969–976.

- Waring, R.H., Schlesinger, W.H., 1985. Forest Ecosystems: Concepts and Management. Academic Press, San Diego, CA, pp. 263–276.
- Waring, R.H., Landsberg, J.J., Williams, M., 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.* 18, 129–134.
- Wesely, M.L., Hart, R.L., 1985. Variability of short term eddy-correlation estimates of mass exchange. In: Hutchinson, B.A., Hicks, B.B. (Eds.), *The Forest–Atmosphere Interaction*. D. Reidel, Dordrecht, pp. 591–612.